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On the Assimilatory System.

G. Haberlandt, in Ber. d. deutsch. bot. Ges., Vol. IV, pp. 206-236, pl. xi., furnishes a valuable contribution to the elucidation of this interesting subject.

E. Stahl and other authors have advanced the theory that the peculiar shape and position of the palisade-cells are due to the influence of insolation. The chlorophyll grains in the layers of the leaf most exposed to the sunlight are said to have the tendency to avoid the intense light of the perpendicular rays by placing themselves along the side-walls of these cells. They will thus assume a profile position, while the granules in the more protected, deeper layers, in the so-called spongy parenchyma, will occupy the walls parallel to the leaf-surface, thereby presenting their broad side to the incident light. This tendency, according to the authors cited, will cause the palisade-cells to elongate in a direction perpendicular to the leaf-surface, so as to afford the chlorophyll grains ample room to assume the most favorable position. The cells on the spongy parenchyma on the other hand will, for the same reason, expand horizontally. Thus the frequent absence of palisade tissue and the more abundant development of the spongy parenchyma in leaves that have grown in the shade would be explained.

When the solar rays strike the surface of a leaf perpendicularly, the migration of the chlorophyll grains to the side-walls of the palisade-cells, can be easily observed *in some plants.** *Ranunculus Ficaria* is said by Haberlandt to be very good for this purpose. The chlorophyll grains will leave the transverse walls completely in about fifteen minutes. It takes several hours, how ever, for them to return to their former position after insolation has ceased. If a cross-section from a leaf that had been insolated for some time is examined, the chlorophyll grains are found distributed rather uniformly on all the side-walls of the palisade-cells. Then, if the sunlight is directed so as to fall perpendicularly on the long sides of these cells, nearly all the chlorophyll grains will gather on those side-walls which lie in the same plane as the

*Prothallium of ferns, *Vaucheria* (Stahl), *Ornithogalum nutaus and umbellatum*, *Muscari racemosum*, *Scilla bifolia*, etc.

incident rays, *i. e.*, they will assume the profile position ; a few grains will pass to the transverse walls.

If in all plants, or, at least, in very many, the chlorophyll grains were affected by the solar light in this manner, Stahl's theory would appear highly satisfactory, but the plants mentioned are rare exceptions. Generally the chlorophyll grains do not change their position, but occupy the side-walls of the palisade-cells without being influenced by the intensity or direction of the sunlight. Even the assumption that the chlorophyll grains of the palisade-cells always present their profile to the incident rays is not correct. There are very many plants the leaves of which have large air-spaces under their stomata. These spaces are bordered by palisade-cells that have their lower side-walls curved, frequently even horizontal. Now these horizontal portions of the side-walls are found covered with chlorophyll grains during the most intense insolation, when the granules must necessarily present their broad side to the incident rays. *Scilla bifolia* furnishes a very good illustration.*

Frequently some palisade-cells will be found projecting with their free, upper end into the air-spaces mentioned. In such cells the uppermost transverse wall is often densely covered with chlorophyll grains, although it is parallel to the surface of the leaf. Besides, it must be considered that the rays when passing through the epidermis are doubtless much refracted and dispersed, so that we cannot positively say at what angle they fall upon the chlorophyll grains. We know that in the open air, sun rays never rest on a perpendicular leaf for any considerable time.

If, therefore, for all these reasons, the profile position of the chlorophyll grains in relation to the incident rays cannot be considered as the normal one, it follows that the peculiar expansion of the palisade-cells at right angles with the leaf-surface must not necessarily have been developed simply to afford the chlorophyll grains greater facility in assuming that position.

The author proceeds to show that no chlorophyll grains are found on the walls separating the palisade-cells from the cells of the next lower layer, and that, in this respect, it makes no difference whether these cross-walls are vertical, oblique, or horizontal.

* I examined *Urginea Scilla* (*S. maritima*) with the same result.

As the current carrying along the products of assimilation,—the carbohydrates—passes through these walls on its way to the conductive parenchyma surrounding the fibro-vascular bundles, it appears, so the author reasons, that the chlorophyll grains avoid those walls, so as not to obstruct that current. Consequently the other walls, *i. e.*, the side-walls, must furnish space for the chlorophyll grains, hence their enlargement in the direction of the current.

In the third and fourth sections of the article the author adds a considerable amount of material against Stahl's (and Pick's) theory. The most important fact he adduces seems to be, that palisade tissue is formed on both sides of leaves growing horizontally, and that some leaves, although they have grown in deep shade, will produce such tissue even on their lower side. This certainly seems to tell against the theory that the development of palisade tissue is dependent on the intensity of insolation.

The last section is devoted to the discussion of the author's own theory, according to which the assimilatory tissue is constructed on a plan that permits the transportation of the products of assimilation the most direct way and in the shortest possible time. The radial arrangement of the chlorophyll-carrying cells in *Cyperus*, several grasses, and *Equisetum* is illustrated and explained, in order to demonstrate that the direction of the current within the cells, not their position relative to the surface of the organ to which they belong, determines their shape and size.

* * *

When I read Haberlandt's paper and wrote an abstract of it for the BULLETIN, the theory advanced in it seemed to me very plausible indeed. But after having carefully examined the leaf of *Urginea Scilla*, both during insolation and after long continued exclusion of light, I find that in many palisade-cells chlorophyll grains are found on the cross-partitions. In fact, I cannot see how the presence of a few granules at those walls could materially obstruct the passage of the sap-current.

I venture to suggest that neither Stahl's nor Haberlandt's theories are necessary to explain the structure of the palisade-cells. It is agreed, I think, that an indispensable factor in the process of assimilation is the atmospheric air. The chlorophyll

grains place themselves, with decided preference, along the walls bordering on the intercellular air-spaces* with which the tissues of the leaf are freely interspersed. (In this respect the leaf of *Scilla* is especially instructive; a transverse section parallel to the nerves shows that numerous air-passages are found not only underneath the stomata, but between the contiguous vertical walls of the palisade cells. Even such leaves which, at first sight, seem to have no interstices between their palisade-cells, e. g. *Pilocarpus*, *Actostaphylos* and *Senna*, will be found to contain very narrow, but numerous air-passages along their vertical walls, especially if sections parallel to the leaf-surface be examined).

At the same time each cell of the assimilatory layers feels compelled, as it were, to struggle for its share in the sunlight, the source from which it receives all its energy.

How can we imagine a plan better adapted to fulfil these two conditions, than that on which the palisade tissue is constructed? Into a given volume of this tissue the greatest possible number of cells is packed in such a manner that each presents its upper surface to the incident rays, permitting them to pervade its whole interior, while, at the same time, it furnishes ample accomodation to the chlorophyll grains, on its long walls, where they have the best opportunity to come into contact with the carbonic acid in the air passages. Whether the sun rays strike the profile or the face of the chlorophyll grains is indifferent (as shown by Haberlandt), but whether some grains lie in the path of the sap-current or not, seems to be immaterial also. We shall, of course, most likely not find many chlorophyll grains along the cross-partitions, because there are no air passages adjoining those walls.

That in leaves growing in the shade the palisade-tissue is not developed at all, or not so freely as in leaves exposed to direct sunlight, might simply be explained by the consideration that the force of one of the factors, producing the peculiar growth of the palisade-cells, is considerably diminished. In all organisms the development of such parts is retarded or checked, which, for some reason or other, are prevented from fully performing their functions.

JOS. SCHRENK.

* Frank in Pringsh. Jahrb. f. Bot., Vol. VIII., p. 299.